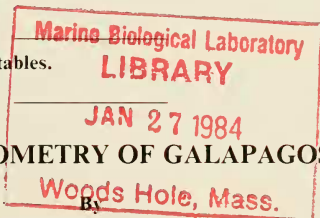


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THE CRANIAL MORPHOMETRY OF GALAPAGOS TORTOISES



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**ABSTRACT:** Saddlebacked tortoises have smaller and slightly broader skulls than non-saddlebacked tortoises. Unlike the two types of shells, the skulls of saddlebacked and non-saddlebacked tortoises are difficult to distinguish, even as large adults. Factor analysis, although suggestive of different growth trends, does not delineate *Geochelone ephippium*, *G. guntheri*, and/or *G. nigrita*. Discriminant function analysis easily distinguishes these species. *Geochelone ephippium* is discriminated from the other two species on the basis of overall size and *G. nigrita* has a smaller exposed basisphenoid than *G. guntheri*. Species represented by small samples were compared to *Geochelone guntheri*, *G. ephippium*, and *G. nigrita* by means of a discriminant function analysis classification procedure. The results suggest that skull variation does not parallel shell variation.

INTRODUCTION

The classification of Galapagos tortoises (genus *Geochelone*) has changed over the years, depending on the prevalent philosophy pertaining to closely related forms. These insular tortoises have been considered different species (Van Denburgh 1914) or different subspecies (Wermuth and Mertens 1961, 1977; Crumly 1980, 1982; MacFarland et al. 1974a, b). Perhaps the best a priori taxonomic strategy was employed by Fritts (*in press*), who considered each geographically isolated population a separate entity until more detailed analysis could be completed. These different philosophies, compounded by the frequent lack of accurate locality data, are reflected in the confusing nomenclatural history of Galapagos tortoises (Table 1).

Although the nomenclatural status of these various populations remains changeable, it is clear that all Galapagos tortoises are more closely related to each other than to other tortoises. This interpretation is supported by morphologic analyses (Crumly 1980, 1982; Fritts *in press*) and electrophoretic studies (Marlow and Patton 1981).

Despite their close relationships, Galapagos tortoises exhibit great structural diversity. The shells best reflect this diversity and are of two basic types: domed, like those of most other tortoise species; and saddlebacked, resembling an ancient Moroccan saddle. The saddlebacked shell type seems derived from the domed type, but Fritts (*in press*) has noticed subtle differences between saddlebacked forms that suggest this morphology evolved more than once. Marlow and Patton (1981) corroborate Fritts's suggestion. Furthermore, the saddlebacked shell, long considered unique to certain Galapagos tortoises, appears independently in *Geochelone vosmaeri*

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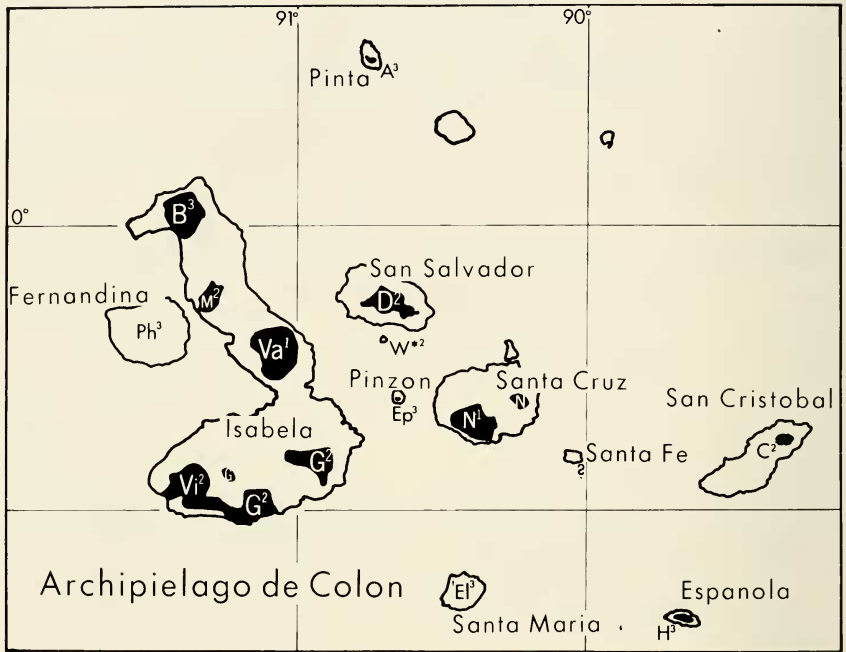


FIGURE 1. Present distribution of *Geochelone* species in the Galapagos Islands. A = *abingdonii*, B = *becki*, C = *chathamensis*, D = *darwini*, E1 = *elephantopus*, Ep = *ephippium*, G = *guntheri*, H = *hoodensis*, M = *microphyes*, N = *nigrita*, Ph = *phantasticus*, Va = *vandenburghi*, Vi = *vicina*, W = *wallacei*, ? = unnamed form, 1 = domed, 2 = intermediate, 3 = saddlebacked, \* = species probably invalid (from MacFarland et al. 1974a).

of Rodrigues Island in the Indian Ocean (Arnold 1979).

Fritts (*in press*) showed that island (or volcano) topography is a reliable predictor of shell shape in Galapagos tortoises. Based on captive breeding data, he also suggested that shell differences are genetically determined. The topographic, climatic, and morphologic information combined in Fritts's model suggests that these tortoises possess great adaptive plasticity. This plasticity, reflected in differences in shell shape, has not been documented for other anatomical regions.

The purpose of this study is to determine whether variation in cranial morphometry parallels variation in the two shell types, first proposed by Van Denburgh (1914) and corroborated by Fritts (*in press*).

#### MATERIALS AND METHODS

Sixteen measurements (Fig. 2, Table 2) were recorded from over 100 skulls, listed below. (The museum acronyms used are those recommended by Duellman et al. 1978.)

- G. abingdonii*: CAS 8112; USNM 29269.
- G. becki*: CAS 8120.
- G. chathamensis*: CAS 8127, 8128, 8130, 8131, 8133; USNM 29255.
- G. darwini*: CAS 8106, 8108, 39601.
- G. ephippium*: AMNH 93383; CAS 8299, 8313, 8358, 8377-8380; MCZ 11068; USNM 29309, 29251.
- G. guntheri*: CAS 8225, 8267, 8413, 8406, 8401, 8399, 8400, 8396, 8415, 8256, 8408, 8405, 8199, 8194, 8210.

TABLE 1. SPECIFIC NAMES APPLIED TO GALAPAGOS TORTOISES.\*

Island name		Carapace type	Günther 1875, 1877	Rothschild 1901, 1902, 1903, 1915	Van Denburgh 1907, 1914	Garman 1917	Wermuth and Merens 1961, 1977	MacFarland et al. 1974	Pritchard 1979
Spanish	English								
Espanola	Hood	Saddlebacked	microphyes	hoodensis	hoodensis	microphyes	hoodensis	hoodensis	hoodensis
Fernandina	Narborough	Saddlebacked		phantastica	phantastica		phantastica	phantastica	phantastica
Isabela	Albemarle	Saddlebacked		becki	becki	macrophyes	elephantopus	becki	becki
	N. Albemarle (Cape Berkeley)								
	Tagus Cove								
	S.E. Albemarle (Villamil ML)	Intermediate		microphyes	microphyes	macrophyes & microphyes	elephantopus	microphyes	microphyes
	S. Albemarle (Iguana Cove)	Intermediate	vicina	guntheri	guntheri	microphyes	elephantopus	guntheri	guntheri
	Cowley Mt.	Domed		vicina	vicina	microphyes	elephantopus	vicina	vicina
				distinctive but not named	distinctive but not named		elephantopus	vandenburghi	vandenburghi
Pinta	Abingdon	Saddlebacked	abingdonii	abingdonii	abingdonii	elephantopus	abingdonii	abingdonii	abingdonii
Pinzón	Duncan	Saddlebacked		ephippium	ephippium	elephantopus	ephippium	ephippium	ephippium
Rábida	Jervis	Intermediate		wallacei	wallacei	nigra	wallacei	wallacei**	wallacei
San Cristóbal	Chatham	Intermediate	distinctive but not named	chathamensis	chathamensis	microphyes	chathamensis	chathamensis	chathamensis
San Salvador (Santiago)	James	Intermediate	elephantopus or nigrita	darwini	darwini	nigrita	darwini	darwini	darwini
Sanja Cruz	Indefatigable	Domed	distinctive but not named	porteri	porteri	nigra	nigrita	porteri	porteri
Santa María (Floreana)	Charles	Saddlebacked	ephippium	galapagoensis	elephantopus	nigrita	galapagoensis	galapagoensis	galapagoensis

\* Fritts (*in press*) is in the process of revising the classification and taxonomy of Galapagos tortoises.

\*\* These authors have convincingly shown that *wallacei* is invalid because tortoises probably never occurred naturally on Rabida.

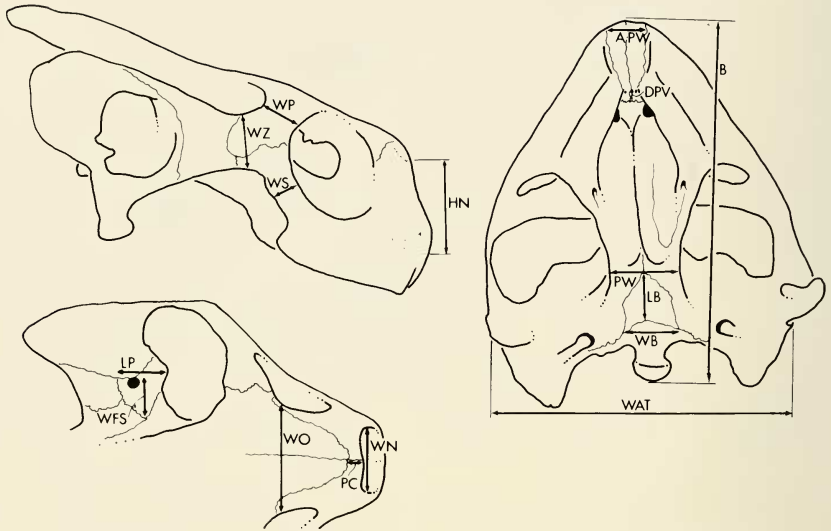


FIGURE 2. Measurements taken from Galapagos tortoise skulls (see Table 2 for explanations of abbreviations).

*G. hoodensis*: CAS 8121, 8122.  
*G. microphyes*: CAS 8158.  
*G. nigrita*: CAS 8381, 8289, 8286, 8385; MVZ 67613–67615, 59528, 67624–67629, 67631–67633; USNM 104330–104331.  
*G. phantastica*: CAS 8101.  
*G. vandenburghi*: CAS 8141.  
*G. vicina*: CAS 8179, 8193, 8177; USNM 129247.  
*G. wallacei* (probably an invalid form, *vide* MacFarland et al. 1974a): CAS 8134.  
*Geochelone* sp. (but definitely Galapagos tortoise species): AMNH 7288, 42961, 63415, 36420, 36568–36570, 63416; CAS 8298, 8404, 8411, 8409, 8402, 8377, 8407, 8410, 8403, 8414, 8397, 8412, 8272; Calif. State Univ., Fullerton Coll. 3 uncat.; FMNH 13523, 1 uncat.; LACM (Vert. Paleol.) pr 63, pr 58, pr 64; MCZ 46606, 11070, 11069, 32098, 1905, 4668; MVZ 80075; SDSNH 56605, 55458; USNM 65896, 102904, 129393, 15192, 29338, 29305, 29254, 29252, 15190, 15193, 29256.

Means and standard deviations were calculated for each of the 16 measurements and correlation coefficients were also calculated.

At the recommendation of Fritts (pers. comm.), I followed the last thorough taxonomic review

(Van Denburgh 1914) in which the different forms were given species-level designations. The species names used by Van Denburgh (1914) are followed with one exception; *G. porteri* is considered a junior synonym of *G. nigrita* (*vide* Fritts *in press*). Statistical comparisons between island

TABLE 2. SKULL MEASUREMENTS RECORDED FOR GALAPAGOS TORTOISES. (All measurements taken with dial calipers and recorded to nearest 0.01 mm.)

Variable—Description

B	Basicranial length
WAT	Width of skull at anterior tympanic opening
WO	Width between orbits
HN	Height of external narial opening
WN	Width of external narial opening
LB	Length of basisphenoid
WB	Width of basisphenoid
WZ	Width of quadratojugal
WP	Width of postorbital
WS	Width of jugal
DPV	Distance (greatest) from prepalatine foramina (or foramen, if only one present) to vomer
LP	Length of prootic
WFS	Width of prootic at stapedial foramen
PW	Width of pterygoid waist
APW	Width of anterior premaxillae
PC	Length of sagittal contact of prefrontals

TABLE 3. MEANS AND STANDARD DEVIATIONS FOR 16 VARIABLES IN FIVE GALAPAGOS TORTOISE SPECIES. MEASUREMENTS ARE ILLUSTRATED IN FIGURE 2 AND ABBREVIATIONS ARE LISTED IN TABLE 2. MOST SAMPLE SIZES ARE SMALL; ALL MEASUREMENTS ARE IN MILLIMETERS.

Variable	<i>G. ephippium</i> (N = 9)		<i>G. guntheri</i> (N = 15)		<i>G. nigrita</i> (N = 18)		<i>G. vicina</i> (N = 4)		<i>G. chathamensis</i> (N = 6)	
	X	SD	X	SD	X	SD	X	SD	X	SD
B	96.7	11.4	128.0	21.4	121.5	39.2	109.0	49.2	98.1	27.3
WAT	73.9	9.2	106.6	19.9	98.4	31.8	86.0	38.9	80.4	25.0
WO	25.1	3.1	35.4	7.3	37.0	13.3	28.4	12.6	28.4	7.7
HN	12.5	2.0	18.6	3.4	18.6	6.0	16.1	7.3	13.9	4.1
WN	17.0	2.2	25.1	4.4	23.1	7.7	21.3	9.2	18.5	4.7
LB	13.3	3.2	18.7	4.2	14.7	4.3	18.1	8.9	14.7	5.6
WB	14.6	2.2	19.1	4.3	17.1	4.6	15.8	7.2	13.8	3.4
WZ	9.3	3.6	14.3	4.4	13.3	4.7	12.6	6.8	10.1	3.5
WP	7.0	2.2	9.5	2.5	9.0	3.5	8.8	4.5	7.3	3.0
WS	7.3	2.3	12.0	3.0	9.5	4.0	9.6	5.1	7.9	3.1
DPV	3.2	0.8	4.2	0.8	4.2	1.5	3.7	2.4	3.1	1.0
LP	14.1	2.1	21.0	5.6	18.1	6.5	14.8	6.6	15.2	3.7
WFS	10.0	2.0	16.0	6.1	12.8	6.1	8.9	6.3	12.5	6.2
PW	19.2	1.8	25.9	5.1	26.1	8.4	21.9	8.6	19.0	4.0
APW	10.5	1.8	15.2	2.4	14.1	4.9	11.8	8.0	10.5	3.0
PC	8.6	1.5	10.6	4.0	13.3	5.4	8.5	3.9	8.2	3.9

populations were hampered by incomplete locality data; 50 of 116 specimens (43%) examined possessed doubtful or unknown locality data. The specimens without locality data were readily identified as Galapagos tortoises, but could not be identified to species without locality data. These specimens were used in the computation of correlation coefficients and in factor analysis, but could not be used in other statistical procedures.

To facilitate my analyses, populations were combined based on the shell types advocated by Van Denburgh (1914) and Fritts (*in press*). Thus, the saddlebacked forms (*G. abingdonii* [N = 2], *G. phantastica* [N = 1], *G. becki* [N = 1], *G. hoodensis* [N = 2], and *G. ephippium* [N = 9]) were combined, yielding a sample of 15 individuals. The non-saddlebacked forms (intermediate and domed shells of Van Denburgh 1914) were also combined, forming a larger sample of 48 individuals (*G. chathamensis* [N = 6], *G. darwini* [N = 2], *G. guntheri* [N = 15], *G. microphyes* [N = 1], *G. nigrita* [N = 18], *G. vicina* [N = 4], and *G. vandenburghi* [N = 1]). These larger samples were then compared to determine whether cranial variation mirrored the already well known shell variation. Comparisons were also made among *G. ephippium*, *G. guntheri*, and *G. nigrita* to determine whether noncombined and combined samples contained the same magnitude of variation.

The Statistical Package for the Social Sciences (SPSS) was used on the WYLBUR facility at the Campus Computer Information Service (CCIS) at Rutgers—The State University for initial data examination. Final statistical analyses were accomplished using SPSS programs available

TABLE 4. MEANS AND STANDARD DEVIATIONS FOR SADDLEBACKED TORTOISES REPRESENTED BY SPECIMENS OF FIVE SPECIES AND NON-SADDLEBACKED TORTOISES REPRESENTED BY SPECIMENS OF SEVEN SPECIES. MEASUREMENTS ARE ILLUSTRATED IN FIGURE 2 AND ABBREVIATIONS ARE LISTED IN TABLE 2; ALL MEASUREMENTS ARE IN MILLIMETERS.

Variables	Saddlebacked (N = 15)		Nonsaddlebacked (N = 48)	
	X	SD	X	SD
B	98.9	15.9	116.5	37.1
WAT	75.8	13.0	96.0	30.4
WO	26.4	4.6	32.9	11.2
HN	13.2	2.9	17.1	5.6
WN	17.5	2.4	22.6	7.2
LB	13.8	3.2	16.0	5.7
WB	14.5	2.0	17.1	5.5
WZ	9.5	3.4	13.1	5.3
WP	7.1	2.2	8.8	3.5
WS	7.3	2.3	9.9	3.9
DPV	2.9	1.2	3.9	1.4
LP	14.4	2.7	18.4	6.2
WFS	10.1	1.8	13.7	6.4
PW	20.1	2.9	24.6	7.8
APW	10.5	1.7	13.2	4.5
PC	7.9	1.4	10.2	5.2

TABLE 5. CORRELATION COEFFICIENTS BETWEEN ALL THE SKULL MEASUREMENTS ILLUSTRATED IN FIGURE 2 AND ABBREVIATED IN TABLE 2. All specimens measured are combined into a single sample. Nevertheless, all coefficients are significant to at least the  $P = 0.05$  level.

Variable	B	WAT	WO	HN	WN	LB	WB	WZ	WP	WS	DPV	LP	WFS	PW	APW
WAT	.98														
WO	.94	.94													
HN	.96	.94	.93												
WN	.97	.96	.93	.95											
LB	.88	.86	.79	.84	.88										
WB	.92	.92	.87	.88	.92	.87									
WZ	.84	.86	.86	.81	.87	.78	.84								
WP	.87	.86	.88	.83	.87	.79	.80	.88							
WS	.91	.92	.87	.88	.91	.86	.89	.84	.84						
DPV	.69	.69	.69	.64	.72	.60	.68	.64	.66	.66					
LP	.95	.94	.91	.91	.94	.85	.91	.86	.84	.91	.63				
WFS	.90	.89	.87	.86	.89	.84	.85	.78	.77	.87	.55	.91			
PW	.92	.91	.90	.90	.91	.78	.88	.85	.83	.83	.69	.90	.82		
APW	.93	.93	.89	.91	.94	.84	.89	.82	.83	.89	.68	.86	.82	.85	
PC	.60	.56	.55	.63	.60	.38	.49	.43	.48	.48	.49	.55	.50	.54	.59

through the Office of Computer Services (OCS) at the Smithsonian Institution. Simple descriptive statistics, linear regression, factor analysis, and stepwise discriminant analyses were used to summarize observed cranial variation.

#### RESULTS

*Geochelone ephippium* appears to have the smallest skull and *G. guntheri* the largest skull of Galapagos tortoises (Table 3), but when maximum basicranial lengths (mean plus two standard deviations) are compared, *G. nigrita* appears to possess the largest skull ( $B_{\max} = 171$  mm for *G. guntheri*, 200 mm for *G. nigrita*). The efficacy of this procedure is in some doubt since the  $B_{\max}$  for *G. vicina* exceeds that of *G. nigrita*, even though no skull of the former is anywhere near as large as the latter. This may be the product of a small sample size for *G. vicina*, represented by only four specimens. The largest skulls in these samples are *G. ephippium*, 114.0 mm; *G. guntheri*, 157.7 mm; *G. nigrita*, 157.6 mm; and *G. vicina*, 142.7 mm. The *G. nigrita* sample includes the two smallest tortoises measured, which depresses the mean basicranial length and elevates the standard deviation.

Combined samples clearly show a size differential between saddlebacked and domed tortoises; saddlebacked tortoises have smaller skulls. This is supported by all 16 variables (see Table 4).

All correlation coefficients were significant to at least the  $P = 0.05$  level (Table 5). Some vari-

ables, however, did not correlate as highly with other variables. Examples include PC, DPV, and LB. Because intervariable correlation was so high, linear regression showed slight, if any, tendency toward curvilinearity. The intercepts for saddlebacked forms were lower than the intercepts for non-saddlebacked forms, reflecting the difference in size between the two groups. Slopes, however, were practically identical. As an example, linear equations relating WO to LB for saddlebacked and non-saddlebacked tortoises have slopes of 1.38 and 1.37, respectively, whereas intercepts are 7.92 and 11.74, respectively ( $r = 0.75$  for saddlebacks and 0.69 for nonsaddlebacks,  $P \leq 0.005$  for both).

Factor analysis yielded three factors, the first accounted for almost 95% of the data variance (see Table 6). Before rotation all 16 variables correlated most highly with this first factor. Rotation simplifies vectors derived by the analysis procedure and is necessary because factor analysis problems have more than one solution. There are two general rotation techniques: orthogonal and oblique. Orthogonal rotation solutions derive vectors along axes of data variation that are perpendicular to one another and thus uncorrelated. Oblique techniques, on the other hand, do not require that vectors be orthogonal, so vectors can be correlated. Even after varimax rotation, an orthogonal technique that simplifies the columns of a factor matrix by maximizing factor-variable loadings, 12 of the 16 variables correlate most highly with factor one. Varimax rotation

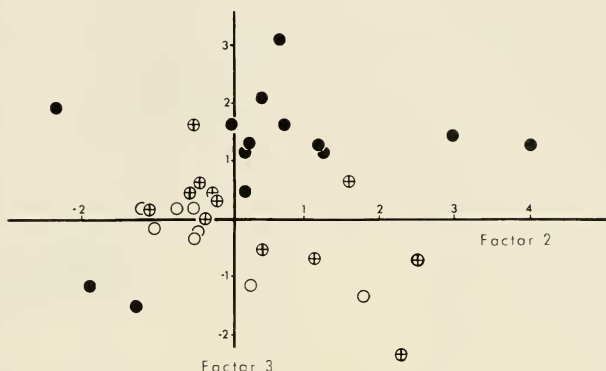


FIGURE 3. A plot of factor scores for factors two and three. *Geochelone nigrita* (solid circles), *G. guntheri* (cross-hatched circles) and *G. ephippium* (open circles). When factor scores for all tortoises are plotted there is a prominent trend from the lower-left to upper-right quadrant. Although this general trend for all tortoises is suggestive of a positive trend toward increased snout elongation with increased robustness (as illustrated by *G. nigrita*), the points for *G. ephippium* and *G. guntheri* show a negative relationship between robustness and snout elongation.

was chosen because it maximizes the variation accounted for by the factor vectors without all the variables loading highly on the same factor, as occurs in quartimax rotation.

Identifying vectors of data variation is speculative; but it seems likely that factor one summarizes variation in size. Thus, 95% of the variation in Galapagos tortoise skulls may be the result of variation in size. The other two factors are more difficult to interpret, partly because so little variation (only 5%) is summarized by these factors. Factor two summarizes variation in cra-

onial width and the width of skull arches, emphasizing WO, WP, WZ, PW, and DPV. Therefore, factor two could be identified as some measure of robustness. Factor three, emphasizing PC and HN, suggests there is variation in the anterior part of the skull. A high factor three score results from an increase in PC and HN. This results from elongating the anteromedial portion of the triturating surface, which concomitantly yields a longer skull.

A bivariate plot of the second and third factor scores for *G. nigrita*, *G. guntheri*, and *G. ephippium* (Fig. 3) indicates that as skulls become more robust, the anterior nasal part of the skull elongates; as robustness increases the skull becomes relatively longer. However, examining the individual points for *G. guntheri* and *G. ephippium* suggests just the opposite: as robustness increases elongation decreases. This negative relationship seems more pronounced in *G. guntheri*.

Three separate discriminant function analyses were done: one for *G. nigrita*, *G. ephippium*, and *G. guntheri*; one for the combined samples; and one comparing small samples to larger samples. In the first analysis, the three forms were distinguished by two factors (Table 7). Factor one summarized variation in 14 of the 16 variables but accounted for only 54.9% of the data variance. A high canonical correlation coefficient and a low Wilks's lambda indicate that this factor is good

TABLE 6. STATISTICS PRODUCED BY FACTOR ANALYSIS USING VARIMAX ROTATION. All specimens were included in this analysis. Abbreviations used in the summarized factor matrix are listed in Table 2. Eigenvalues are measures of the relative importance of the factors.

Factor	1	2	3
Eigenvalue	13.19	0.47	0.28
% Variation	94.6	3.4	2.0
Summarization of Factor Matrix	WFS 0.82 LB 0.80 LP 0.78 WAT 0.76 WS 0.76 B 0.76 WB 0.75 WN 0.73 HN 0.72	WP 0.63 DPV 0.60 PW 0.53 WO 0.53 WZ 0.72	PC 0.75 HN 0.51



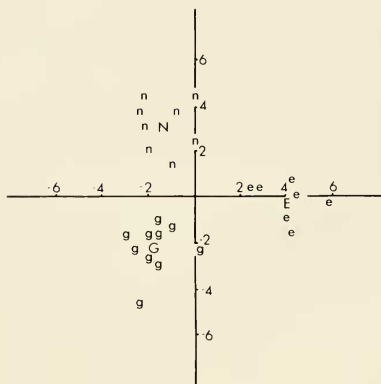


FIGURE 4. A plot of the discriminant scores derived from an analysis that included *Geochelone guntheri*, *G. nigrita*, and *G. ephippium*. Discriminant factor one is the horizontal axis and discriminant factor two is the vertical axis. Statistical separation of these three populations is marked. High positive scores along the horizontal axis indicate small size, whereas high positive scores along the vertical axis indicate a poorly exposed basisphenoid. Upper case letters indicate group centroids.

at distinguishing groups. *Geochelone ephippium* is separated from the other two forms by this factor. The discriminating variables are negatively correlated to factor one, and the species with a small skull is differentiated from the two species with large skulls, suggesting that factor

TABLE 7. STATISTICS PRODUCED BY A DISCRIMINANT ANALYSIS OF *G. ephippium*, *G. guntheri* AND *G. nigrita*. Abbreviations are listed in Table 2. Eigenvalues are measures of the relative importance of the factors; high canonical correlation coefficients (near 1) and low Wilks's lambdas (near 0) indicate that factors are good discriminators.

Discriminant function	1	2
Eigenvalue	7.06	5.82
% Variation	54.8	45.2
Canonical correlation	0.94	0.92
Wilks's lambda	0.02 ( $P = 0.003$ )	0.15 ( $P = 0.02$ )
Pooled within groups correlations bet. canonical	HN -0.22 LP -0.20 WN -0.19	LB -0.21 WB -0.17
discr. fncts. & discr. variables	WAT -0.19 APW -0.18 WO -0.18	
Groups delineated from others	<i>G. ephippium</i> from <i>G. guntheri</i>	<i>G. nigrita</i>

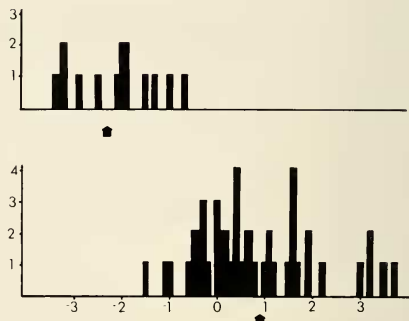


FIGURE 5. A histogram illustrating the results of a discriminant analysis of the saddlebacked and non-saddlebacked forms. The saddlebacked species are in the upper histogram, the non-saddlebacked species are in the lower histogram. The arrows indicate the median in each class. The discriminant scores (high positive scores indicate large size) are on the lower axis and the number of individuals are represented by left-hand axis. Although the saddlebacked and non-saddlebacked forms are clearly different sizes, there is significant overlap.

one is an inverse measure of size. Factor two, which also has a high canonical correlation coefficient and a low Wilks's lambda, distinguishes *G. nigrita* from *G. guntheri* and accounts for the remaining variation in the data. Two variables are highly correlated with this second factor, LB and WB. *Geochelone nigrita* has high positive values for discriminating factor two, indicating that the basisphenoid is poorly exposed. Figure 4 graphically illustrates the completeness of separation.

Standardized canonical discriminant function coefficients are available upon request. These coefficients can be used to calculate discriminant scores for individual specimens whose identity is unknown; but choices are restricted to the populations originally compared (in this case *G. ephippium*, *G. guntheri*, or *G. nigrita*).

The second discriminant analysis applied to the combined samples. Because only two groups were analyzed, a single discriminating factor was computed. The Wilks's lambda was not low, suggesting that the two groups cannot be easily distinguished. The size differential between saddlebacked and non-saddlebacked tortoises is readily apparent (Fig. 5). Standardized canonical discriminant function coefficients are available upon request.

The third discriminant analysis compared



TABLE 8. CLASSIFICATION RESULTS OF A DISCRIMINANT ANALYSIS CLASSIFICATION PROCEDURE. Individual specimens were classified to one of three species: *G. ephippium* (a saddlebacked species), *G. guntheri* (an intermediate form) or *G. nigrata* (a domed form). Asterisk indicates invalid taxon (*vide* MacFarland et al. 1974a).

Shell type	Trivial name	Sex	Mus. no.	Classified as
domed	<i>vandenburghi</i>	?	CAS 8141	<i>ephippium</i>
intermediate	<i>chathamensis</i>	?	CAS 8133	<i>ephippium</i>
intermediate	<i>chathamensis</i>	?	CAS 8131	<i>ephippium</i>
intermediate	<i>chathamensis</i>	?	USNM 29255	<i>ephippium</i>
intermediate	<i>chathamensis</i>	male	CAS 8127	<i>ephippium</i>
intermediate	<i>chathamensis</i>	?	CAS 8130	<i>ephippium</i>
intermediate	<i>chathamensis</i>	?	CAS 8128	<i>ephippium</i>
intermediate	<i>darwini</i>	female	CAS 8106	<i>ephippium</i>
intermediate	<i>darwini</i>	male	CAS 8108	<i>guntheri</i>
intermediate	<i>microphyes</i>	male	CAS 8158	<i>guntheri</i>
intermediate	<i>vicina</i>	male	CAS 8179	<i>ephippium</i>
intermediate	<i>vicina</i>	female	CAS 8193	<i>ephippium</i>
intermediate	<i>vicina</i>	?	USNM 129247	<i>ephippium</i>
intermediate	<i>vicina</i>	male	CAS 8177	<i>guntheri</i>
intermediate	<i>wallacei*</i>	male	CAS 8134	<i>guntheri</i>
saddlebacked	<i>abingdonii</i>	?	USNM 29269	<i>guntheri</i>
saddlebacked	<i>abingdonii</i>	male	CAS 8112	<i>guntheri</i>
saddlebacked	<i>becki</i>	female	CAS 8120	<i>ephippium</i>
saddlebacked	<i>hoodensis</i>	male	CAS 8121	<i>ephippium</i>
saddlebacked	<i>hoodensis</i>	female	CAS 8122	<i>ephippium</i>
saddlebacked	<i>phantastica</i>	male	CAS 8101	<i>guntheri</i>

small samples of tortoise species to large samples. Small samples were classified by the discriminant function classification procedure to one of three species (*G. guntheri*, *G. ephippium*, *G. nigrata*). The results of this procedure are summarized in Table 8. Some species with intermediate shell types (*vide* VanDenburgh 1914) were classified as saddlebacked species (e.g., *G. chathamensis* was classified as *G. ephippium*), whereas other species with intermediate shell types were classified as *G. guntheri*, an intermediate form. No species was classified as a domed form. Skull variation did not parallel shell variation in any meaningful way.

#### DISCUSSION

Small sample sizes and the paucity of accurate locality data limit the utility of this study. Therefore, samples were combined. (Thorpe, 1976, discusses the ramifications of such procedures.) Because most of the specimens in the United States were examined, this limitation cannot be overcome without costly and time-consuming removal of skulls from skins and stuffed specimens of known provenance.

The choice of a putative ancestral morphotype makes an enormous difference in how one interprets evolutionary processes, patterns, and

mechanisms. The size of the ancestral Galapagos tortoise is not known. Auffenberg (1971) believed that the fossil *Geochelone hesternata* was a likely ancestral candidate for Galapagos tortoises as well as *Geochelone chilensis* from Argentina. The skull of *G. hesternata* is very much like a Galapagos tortoise skull. Although it is not as large as that of the largest of Galapagos domed tortoises, it is larger than that of the small saddlebacked tortoises. Thus, I favor an intermediate-sized ancestor for Galapagos tortoises, perhaps something smaller than *G. guntheri*. If so, then *G. nigrata* is the result of continued gigantism and *G. ephippium* is the result of dwarfism.

Why is there such flimsy coincidence between shell variation and cranial variation in Galapagos tortoises? Zangerl and Johnson (1957) and Zangerl (1969) have intimated that much of the shell variation observed in most species has little effect on an individual's survival or fitness. Fritts (*in press*) has shown the contrary for Galapagos tortoises. But this selection on shell morphology does not seem to apply to skull morphology. What other selective factors could be molding skull morphology?

I tend to agree with Bramble (1971), who felt that biomechanical constraints on chewing are the primary sources of selection upon turtle skulls.

How strong are these selective forces? Selective factors imposed by diet are known to be especially strong in other animals from Galapagos. For example, Boag and Grant (1981) discovered that finches in Galapagos experienced intense selection upon beak size and shape as the result of a one-year drought. Because of the long life of tortoises and their ability to survive long periods without food or water, however, short-term environmental changes such as those described by Boag and Grant are unlikely to affect tortoises as severely.

Another source of selective pressure is possible. During intraspecific agonistic encounters (Fritts, pers. comm.), the victor is the individual capable of raising its head the highest. Could apparent head width also affect the outcome of these battles? Interestingly, the relative head width of *Geochelone guntheri* and *G. ephippium* increases with size. These tortoises inhabit low dry islands (or parts of islands) where carrying capacities of the habitat may be lower and intraspecific competition therefore higher. In contrast, relative head width in *G. nigrita* decreases with size. This tortoise lives on a higher moist island where carrying capacities may be higher and intraspecific competition may not be as intense. Also, this apparent decrease in relative width actually accompanies an increase in the length of the masticatory surface area, perhaps allowing more efficient mastication.

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